

New Pedal Remains of *Megaladapis* and Their Functional Significance

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ABSTRACT New remains of *Megaladapis* from the caves within the Ankarana Range of northern Madagascar and the cave site of Ankilitelolo near Toliara in southwestern Madagascar add considerably to the present sample of pedal remains for this genus. Here we describe and analyze the new pedal material and discuss the function of the *Megaladapis* foot in terms of positional behavior and substrate use. The northern specimens belong to the *M. madagascariensis*/*M. grandidieri* group in terms of size and morphology, whereas the new southwestern fossils are assigned to *M. madagascariensis*. The new specimens demonstrate that the small and intermediate sized *M. madagascariensis* and *M. grandidieri* were very similar in anatomy and inferred locomotor function, findings that also support the prior suggestion that they belong to a single widespread subgenus (*Megaladapis*). The new fossils provide the first examples of many pedal elements and present the first opportunity to analyze the whole pedal complex from associated remains.

The foot of *Megaladapis* is distinctive among primates in numerous features. Intrinsic proportions of the hindlimb indicate that the foot is relatively longer than that of any other primate. The first complete calcanei reveal a large and highly modified hindfoot. The calcaneus is reduced distally, indicating an emphasis on climbing over leaping or quadrupedal walking and running. Proximally, a large, medially directed calcaneal tuberosity suggests both a strong inversion component to plantarflexion and a well-developed abductor mechanism and recalls the calcaneal morphology of the larger lorises in some respects. Talar shape is consistent with considerable tibial rotation during plantarflexion and dorsiflexion. The subtalar joint is designed to emphasize supination/pronation and medial/lateral rotation over proximo-distal translation. The distal tarsals are extremely reduced in length, and they form a high transverse arch and a serial tarsus; this configuration promotes inversion/eversion at the transverse tarsal joint. The phalanges are long and moderately curved, and the hallux is very long, robust, and abducted.

Pedal morphology suggests that *Megaladapis* (subgenus *Megaladapis*) was well adapted to exploit an arboreal environment. The grasping mechanism of *Megaladapis* is an extreme modification of the prosimian condition, emphasizing a highly inverted set, mobility in rotation, and a powerful abduction/

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flexion type grasp using the large hallux and the lateral abductor musculature. Such a mechanism insures a secure grasp regardless of the position of the hindlimb or the substrate. These pedal design features contrast with the grasping strategy seen in the highly arboreal palaeopropithecids (or "sloth lemurs"), a group that reduces and modifies the hindfoot, culminating in *Palaeopropithecus*, and emphasizes extrinsic digital flexors in a more hook-like mechanism. Much less is known of *M. (Peloriadapis) edwardsi*. The larger body size, more gorilla-like talar articular morphology, and anatomy of the proximal fifth metatarsal suggest that this species may have been more terrestrial than the smaller forms, but other aspects of pedal morphology suggest it also exploited arboreal habitats.

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The extinct giant lemur *Megaladapis* has been known to science since the late nineteenth century (e.g., Major, 1893, 1894, 1899, 1900; Grandidier, 1899a,b, 1900a,b, 1902; Lorenz von Liburnau, 1900, 1905; Standing, 1903). The genus contains three recognized species: *M. edwardsi*, *M. madagascariensis*, and *M. grandidieri*. Until recently, these three were usually characterized as size and geographic variants of one another (e.g., Walker, 1967; Tattersall, 1975, 1982; Jungers, 1977, 1978, 1980; Szalay and Delson, 1979; Gebo, 1986a) with the largest (*M. edwardsi*) and the smallest (*M. madagascariensis*) occurring together in the south and southwest of Madagascar, while the "intermediate" (*M. grandidieri*) was known only from the central high plateau. A reevaluation of old and new material suggests instead that there may have been two distinct lineages of *Megaladapis* that differed in geographic distribution, details of morphology, and perhaps behavior (Vuillaume-Randriamanantena et al., 1992). New specimens from the north and northwest, along with bones of *M. grandidieri* and *M. madagascariensis*, can all be included in the subgenus *Megaladapis*, a geographically widespread but anatomically similar group of arboreal folivores. *M. edwardsi*, on the other hand, is better placed in the subgenus *Peloriadapis*, a geographically restricted, large-bodied, and possibly less arboreal, folivorous lemur (Vuillaume-Randriamanantena et al., 1992).

Early assessments of posture and locomotion in *Megaladapis* were plagued by the lack of associated cranial and postcranial remains, especially of the smaller forms. Nev-

ertheless, the positional repertoire and habitat preference of *Megaladapis* has been interpreted in many ways, including arboreal climber-hanger to various extents (Grandidier, 1902, 1905; Lorenz von Liburnau, 1905; Standing, 1908; Lamberton, 1934; Zapfe, 1963; Walker, 1967, 1974; Preuschoft, 1971; Jungers, 1976, 1977, 1978; Tattersall, 1982), terrestrial quadruped (Lamberton, 1939, 1946; Mahé, 1972), and even aquatic (Standing, 1908; Sera, 1938; Hill, 1953).

Early reconstructions of the positional repertoire of *Megaladapis* were influenced by the anatomy of the cheiridia, especially curvature of the pedal and manual phalanges (e.g., Grandidier, 1905; Lorenz von Liburnau, 1905). Until recently, the only known tarsal elements were isolated tali (Lamberton (1939) summarized the available evidence). Lamberton (1939) also noted the curvature of the phalanges in *Megaladapis* and stated that these are designed adequately for climbing; he concluded "... *Megaladapis* étaient des creatures terrestres, mais qu'ils grimpaient occasionnellement dans les arbres..." (p. 100) (translation: *Megaladapis* were terrestrial creatures, but ones who occasionally climbed in trees...). Later, however, in describing two metapodials attributed by him to *M. edwardsi*, Lamberton (1946) emphasized that the foot of *Megaladapis* is more indicative of an animal designed for terrestrial walking than climbing. Walker (1967, 1974) disagreed, arguing that "the foot of *Megaladapis* is typically lemuroid and was obviously a grasping organ, with a strong ab-

ducted hallux and long digits" (1974:375), and he used these features to conclude that *Megaladapis* was probably characterized by "a modified vertical clinging and leaping locomotion in which leaping powers were reduced in favor of large body size (Walker, 1974, p. 375)." In a biomechanical analysis of the metapodials and phalanges attributed to *Megaladapis* and *Palaeopropithecus*, Preuschoft (1971) concluded that the bones of both of these giant subfossil lemuroid primates are designed to resist the stresses generated during climbing.

The first pedal digit of *Megaladapis* has figured prominently in prior assessments of pedal function. Lorenz von Liburnau (1905) figured a bone he believed to be the left first metatarsal of *Megaladapis edwardsi*. Lamberton (1946) subsequently attributed two much smaller metapodials to *M. edwardsi* and believed that those described by Lorenz von Liburnau (1905) did not belong to *Megaladapis* at all. Walker (1967) suggested instead that those described by Lamberton probably belonged to *M. madagascariensis* because of their smaller size. Jungers (1976) argued that they are probably more appropriately assigned as first metacarpals of *M. edwardsi* based on the morphology of the proximal end and their length relative to the other metapodials; he makes the same claim for a metapodial that had formerly been assigned to the foot of *Megaladapis* by Ekblom (1951) because of its similarity to the Académie Malgache specimens described earlier by Lamberton (1946). Ekblom (1951) also described a distal hallucal phalanx assigned to *M. edwardsi*. Jungers (1976) agreed with this attribution and interpreted the relatively large size of this distal phalanx as further support for the suggestion that "the hallux of *Megaladapis* was a very long and strong grasping organ" (p. 218).

American-Malagasy expeditions during the last decade to the caves of the Ankarana Massif in northeastern Madagascar have uncovered numerous remains of *Megaladapis* (Fig. 1). The new material from the Ankarana includes associated cranial and postcranial specimens, including an almost complete skeleton of a subadult *Megaladapis*. Within these new collections are the first known representatives of many pedal

elements of *Megaladapis*, most of which are associated with other elements diagnostic of the genus. The 1994 field expedition to the southwest region of Madagascar yielded many new and previously unknown pedal elements of *M. madagascariensis*. This material includes several isolated adult elements as well as relatively complete and associated hindlimbs of a juvenile *M. madagascariensis*. These new specimens allow the opportunity to reassess the earlier allocation of pedal specimens to *Megaladapis* and to analyze more fully the positional repertoire and substrate use in *Megaladapis* by evaluating grasping and weight-bearing functions of the foot. Furthermore, the new material from the north and southwest enhances our understanding of the range of variation present among the smaller subgenus *Megaladapis*. Here we review the current status of pedal collections of *Megaladapis*, analyze the functional significance of pedal morphology in *Megaladapis*, and compare pedal functional morphology of the three species of *Megaladapis* to other primates. The new material from the north will be referred to here as *Megaladapis* sp. (cf. *madagascariensis/grandidieri*), as the species designation of all the new northern material is unclear, yet it clearly belongs to the larger group referred to as the subgenus *Megaladapis* by Vuillaume-Randriamanantena et al. (1992).

FOSSIL PEDAL REMAINS

New specimens contribute substantially to our knowledge of the pedal skeleton of the small and intermediate-sized *Megaladapis madagascariensis* and *M. grandidieri*, but our inferences about *M. edwardsi* still depend on former acquisitions and interpretations that can be extrapolated from the new material. The recently recovered material of *M. madagascariensis* from the southwestern site of Ankilitelo is remarkably similar to the northern material in both size and morphology. The following descriptions and analyses will include all the material currently known for *Megaladapis* but will emphasize the new tarsal material that provides the first opportunity for analysis of the foot as a whole and as a part of the hindlimb

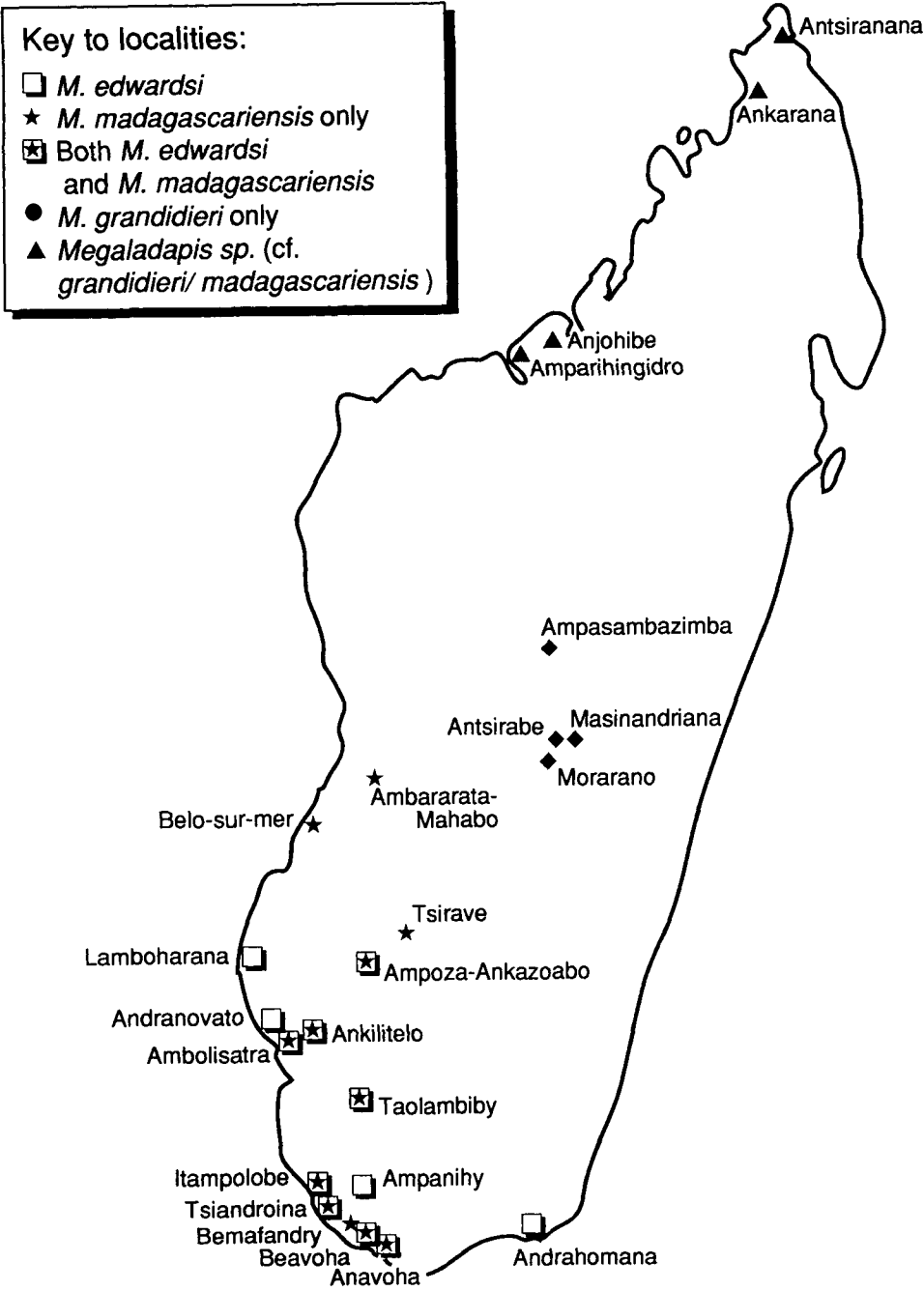


Fig. 1. Map of Madagascar showing fossil localities from which *Megaladapis* remains have been recovered to date. The new remains discussed here are from the cave sites of Ankarana in the north (*Megaladapis* sp. [cf. *madagascariensis*/ *grandidieri*]) and Ankilitelo in the southwest (*Megaladapis madagascariensis*).

TABLE 1. Summary of new *Megaladapis* pedal remains

Catalogue number	Attribution	Site	Specimens
DPC 7950	<i>Megaladapis</i> sp. (cf. <i>madagascariensis</i> / <i>grandidieri</i>)	Ankarana	Calcaneus, left Talus, left Cuboid, right Navicular, left Entocuneiform, left Metatarsal 1, right Metatarsals 4,5, left Assorted phalanges
DPC 7821	<i>Megaladapis</i> sp. (cf. <i>madagascariensis</i> / <i>grandidieri</i>)	Ankarana	Calcaneus, right Talus, right Navicular, right Entocuneiform, right Mesocuneiform, right Ectocuneiform, right Metatarsal 1, right Metatarsal 5, left Assorted phalanges
DPC 9089	<i>Megaladapis</i> sp. (cf. <i>madagascariensis</i> / <i>grandidieri</i>)	Ankarana	Calcaneus, left and right Talus, left and right Cuboid, left and right Navicular, left and right Entocuneiform, left and right Mesocuneiform, left Ectocuneiform, left and right Metatarsals 1–5, left and right Assorted phalanges
DPC 13733	<i>Megaladapis madagascariensis</i>	Ankilitelo	Calcaneus, right Talus, left and right Cuboid, right Navicular, left and right Entocuneiform, left and right Mesocuneiform, left Ectocuneiform, left and right Assorted metatarsals and phalanges
DPC 13739	<i>Megaladapis madagascariensis</i>	Ankilitelo	Calcaneus, right
DPC 13744	<i>Megaladapis madagascariensis</i>	Ankilitelo	Metatarsal 1, right
Uncataloged (Burney, personal communication)	<i>Megaladapis madagascariensis</i>	Belo-sur-Mer	Talus, left

functional complex. Two adult individuals of the intermediate-sized *Megaladapis* from the north, DPC 7950 and DPC 7821, contain a number of associated elements; between the two individuals, every pedal element is represented (Table 1; Fig. 2). Other isolated specimens add to the collection of adult remains. The subadult skeleton, DPC 9089, has two almost complete feet in association with the remainder of the hindlimbs (Fig. 3). The new material of *M. madagascariensis* from Ankilitelo includes almost complete feet from associated hindlimbs of a juvenile individual (DPC 13733) as well as isolated elements from adult individuals.

These new fossils are described below and compared to known specimens. Functional inferences are also offered for joint complexes of the foot.

Calcaneus

The new specimens from the Ankarana provide the first evidence of a calcaneus associated with other *Megaladapis* remains, including one complete and one partial adult calcaneus, and two partial calcanei from the associated subadult skeleton. The new specimens from the southwest include a complete right calcaneus (DPC 13739) and a nearly complete left calcaneus from the associated juvenile hindlimb. The new specimens confirm that the British Museum calcaneus (BM 7946) from Andrahomana, formerly the only calcaneus attributed to *Megaladapis* (Walker, 1967), is not a specimen of this genus (Wunderlich et al., 1993, 1994) (Fig. 4) but probably belongs instead to a large archaolemurine.

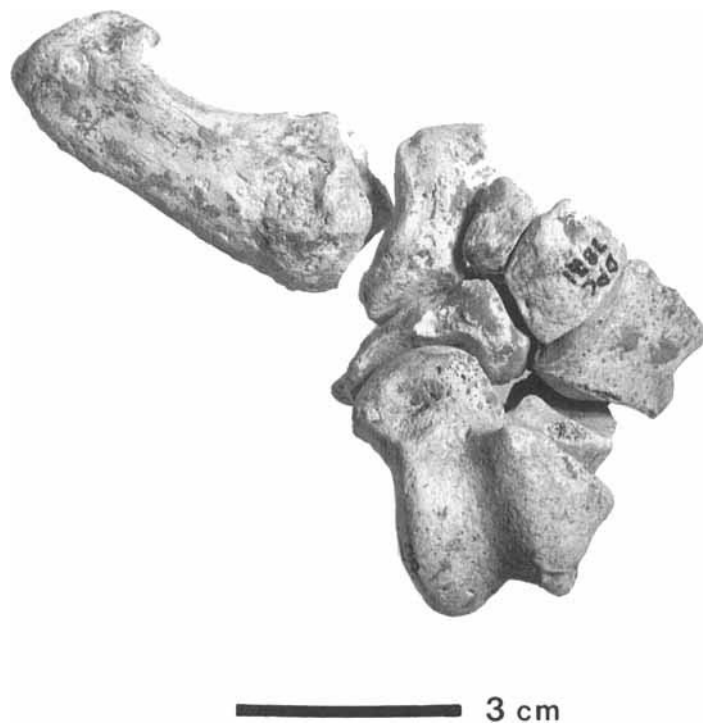


Fig. 2. Composite adult foot (individuals DPC 7950 and DPC 7821) of *M. sp.* (cf. *madagascariensis/grandidieri*) from the north. The proximal end of the calcaneus is broken such that only the distal end is visible where it articulates with the cuboid. Note the abducted position of the hallux, the serial nature of the transverse tarsal joint, and the anteroposteriorly shortened distal tarsals.

The calcaneus of *Megaladapis* (Fig. 4) is long, narrow distally, and curved plantarly. The calcaneus is large relative to the remainder of the pes; *Megaladapis* does not exhibit the extreme hindfoot reduction seen in the subfossil sloth lemurs (Wunderlich et al., 1994) but rather seems to emphasize this element within its grasping mechanism. In intrinsic proportions, the calcaneus is exceptionally short distally and long proximally. Only *Palaeopropithecus* among living and extinct prosimian primates exceeds *Megaladapis* in these proportions (Fig. 12).

The facet for the cuboid is high and narrow and in a ratio of height to width exceeds all living primates; only lorises approach the shape of this joint seen in *Megaladapis*. A shallow depression for the cuboid process is located centrally on the medial surface of the oval-shaped facet. The remainder of the facet is planar inferiorly and laterally but is somewhat sloped superiorly so as to face inferolat-

erally. The facet is bounded inferiorly by a robust plantar tubercle for the attachment of plantar ligaments. The distal facet for the talus is reduced and especially short for its width. It extends to the distal end of the calcaneus, reflecting a serial tarsus in which the joints of the transverse tarsal joint form one continuous joint (Gebo, 1985). The proximal facet for the talus is short and narrow distally but broadens proximally and is strongly offset from the axis of the calcaneus. The sustentaculum tali is narrow and set obliquely to the medial side of the calcaneus such that there is no distinct flexor groove. A peroneal tubercle is present and positioned inferior to the proximal portion of the proximal facet for the talus; despite erosion of this region in all the specimens, this tubercle does not seem to have been very large.

The most distinguishing feature of the *Megaladapis* calcaneus is the extreme medial projection of the proximal heel process.

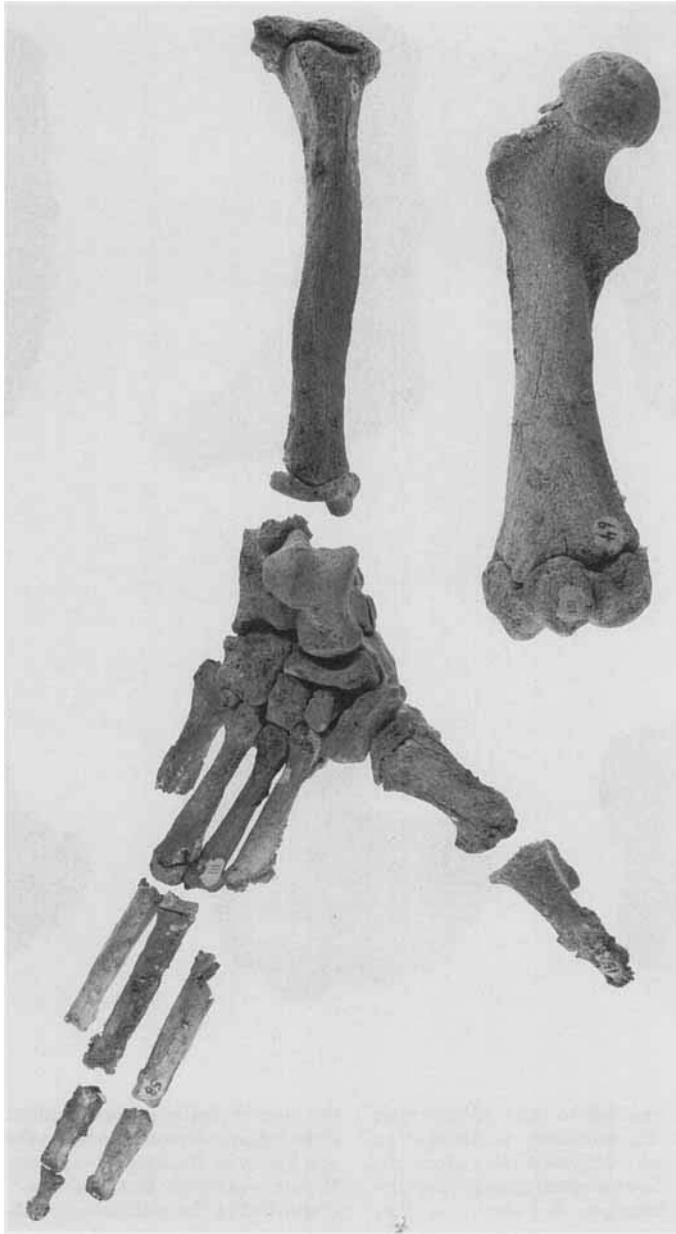


Fig. 3. Associated hindlimb remains of the juvenile *Megaladapis* sp. (cf. *madagascariensis/grandidieri*) (DPC 9089) from the caves of the Ankarana region in the north of Madagascar. The foot of *Megaladapis* is larger relative to its hindlimb than for any other primate. In the reconstruction of the right foot seen here, the posterior portion of the calcaneus is missing, and

the cuboid is positioned distal to its proper area of articulation on the navicular. Prominent features are discussed in the text; note especially the large, abducted hallux, the long and robust metatarsals and phalanges (phalanges not necessarily arranged sequentially), and the anteroposteriorly shortened distal tarsals.

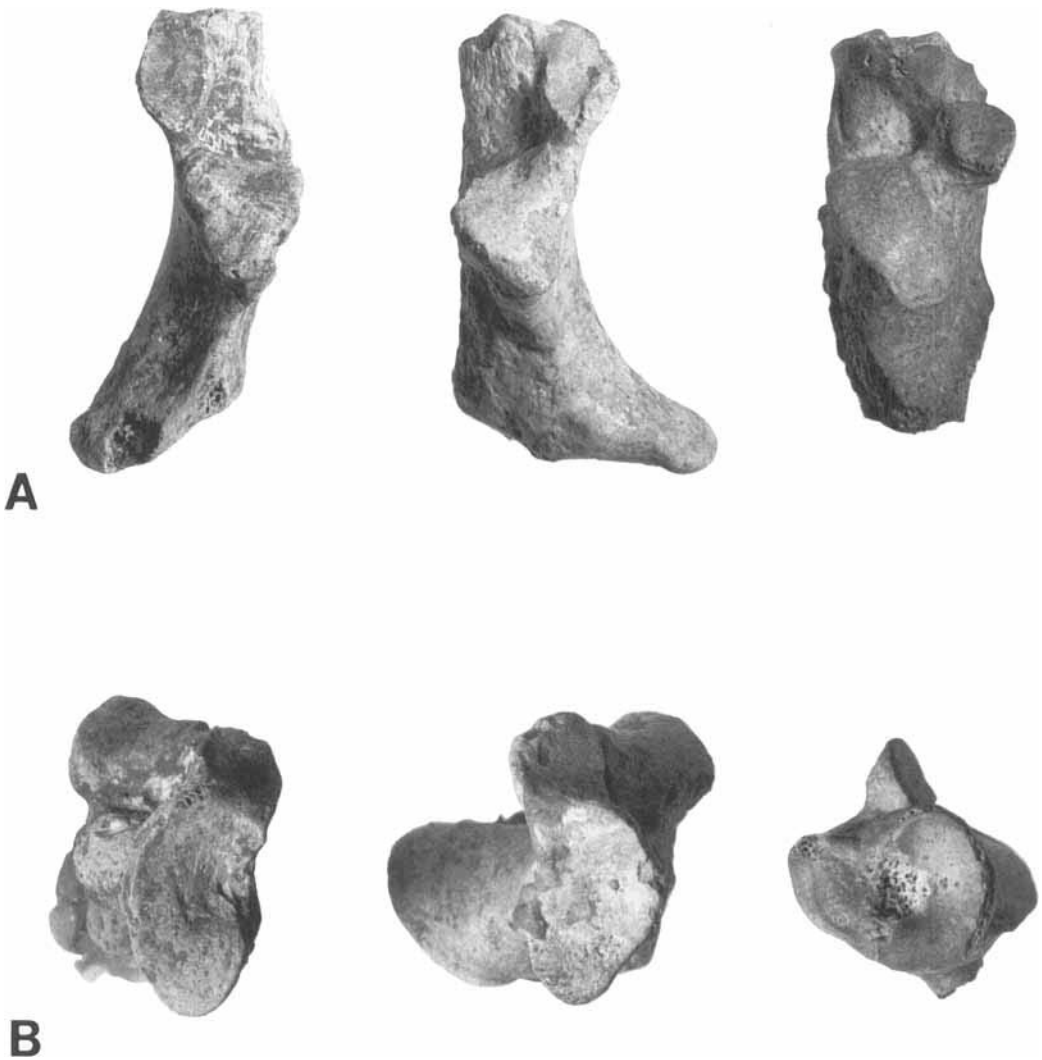


Fig. 4. Calcanei of (from left to right) *Megaladapis madagascariensis* from the southwest of Madagascar. *M. sp.* (cf. *madagascariensis/grandidieri*) from the north, and the British Museum calcaneus (M 7946) formerly attributed to *Megaladapis*. **A:** Dorsal view. Note

the large medially projecting calcaneal tuberosity, the short anterior calcaneus, and the shape of the sustentacular facets in *Megaladapis* as compared to the British Museum specimen. **B:** Distal view. *Megaladapis* is distinguished by the high, narrow cuboid articulation.

Only lorises among extant primates exhibit such a medial heel process, but no other primate possesses this condition to the extent seen in *Megaladapis* (Fig. 4). Although both complete specimens exceed all living primates in the extent of this process, the northern specimen (DPC 7950) exhibits this feature to a much greater extent than the new *M. madagascariensis* (DPC 13739) from

the southwest. Rugose muscle scarring is present on the proximal and plantar surfaces of this process. Proximally, this process would serve as an insertion for the triceps surae tendon, bringing this attachment further medially than is seen in extant forms. The plantar and medial surfaces of this process would have served as an origin for the abductors of the fifth digit. In prosimians

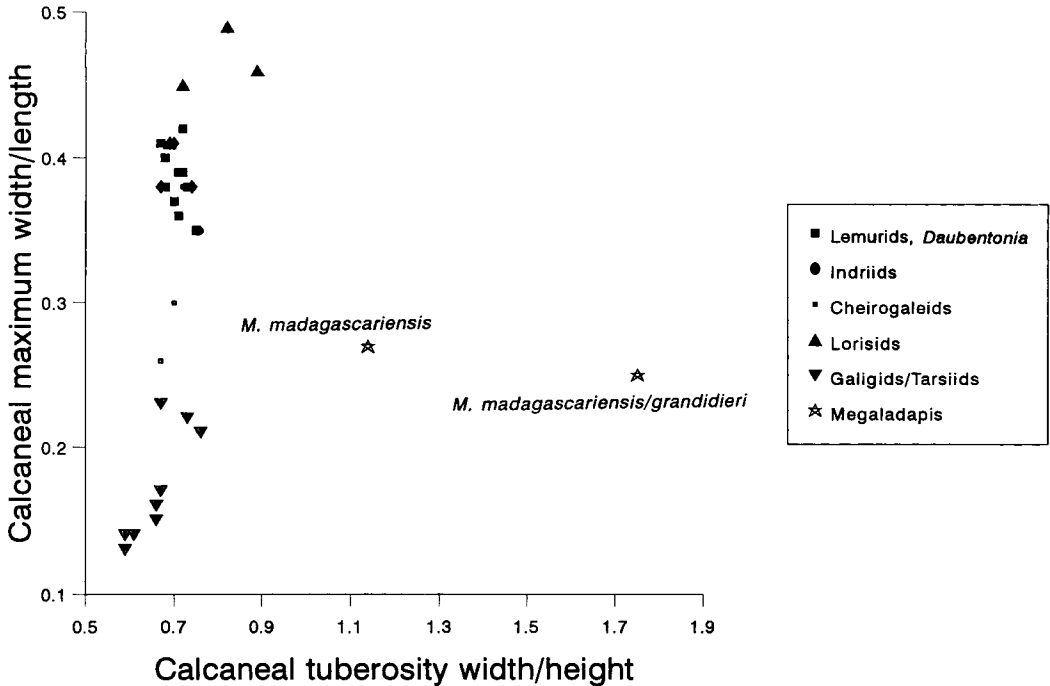


Fig. 5. The most distinguishing feature of the *Megaladapis* foot is the extreme expansion of the calcanear tuberosity. The body of the calcaneus is also narrow relative to most prosimians except the small galagids and tarsiers. As discussed in the text, the medial expansion of the calcanear tuberosity probably served to enhance the actions of the triceps surae muscles proximally and the intrinsic abductors, especially that to the fifth digit, plantarly.

the abductor of the fifth digit takes origin on the medial side of the calcaneus (Fig. 5), whereas in anthropoids this same muscle takes its origin on the lateral side of the calcaneus. In the most common prosimian condition, much of the first and fifth digit abductors take origin from a common raphe which is attached to the medial calcaneus. *Nycticebus* and *Perodicticus* depart from this condition in that their first digit abductor has a distinct origin from the flexor tunnel and underlying sesamoids as well as the navicular tuberosity. While the hallucal abductor has only a very small (if any) bony origin of its own in most prosimians, the fifth digit abductor takes a fan-shaped origin from the medial calcaneus (Gebo, 1985; personal observation by R.E.W.). The large medial process in *Megaladapis* is probably associated with both a medial shift of the triceps surae attachment as well as with enlarged abductors of the fifth and first digits.

The medial insertion of the triceps surae musculature would serve to invert the foot during plantarflexion. When prosimians climb vertical supports, the foot is placed in an abducted (laterally deviated), inverted position. In this position, an animal can augment frictional force through foot-to-foot opposition and grasping. Simultaneous flexion and abduction of the digits serves to increase friction and resist the tendency of gravity to adduct the digits (Cartmill, 1985; Gebo, 1986b; Preuschoft, 1971). When the foot is set in this inverted position, the abductor musculature, especially that of the fifth digit, acts in a line so as to abduct and flex simultaneously and thereby maintain an effective grasp (Gebo, 1985). We believe that this muscular complex was well developed and favorably positioned in *Megaladapis*. Simultaneous inversion and plantarflexion by the triceps surae is also potentially useful in under-branch suspensory situations, in

that it allows "plantarflexion" of the leg on the foot while the latter is fixed in the inverted grasping position.

The calcanei from the north (*M. sp. cf. madagascariensis/grandidieri*) and southwest (*M. madagascariensis*) are remarkably similar in size and overall morphology. In absolute length, the complete adult calcaneus from the north measures 58.1 mm, and the southwestern specimen measures 56.2 mm. The two specimens are also very similar in relative proportions of the calcaneus (see below). The only difference between the two calcanei is the relatively greater medial expansion of the calcaneal process in the northern specimen; however, both specimens show a greater expansion of this process than any living prosimian.

Talus

The talus of *Megaladapis* is the only tarsal element known from all three currently recognized species; isolated tali have been described extensively in the literature and have been commonly described as size morphs of one another (Lorenz von Liburnau, 1905; Lamberton, 1939; Walker, 1967; Dagosto, 1986; Gebo, 1986a). Tali of both *M. edwardsi* and *M. madagascariensis* are known from Beavoha (Lamberton, 1939); *M. edwardsi* is recorded by Lorenz von Liburnau (1905) from Andrahomana; a talus from Ampoza is assigned to *M. madagascariensis* (Walker, 1967)¹; a talus of *M. grandidieri* is known from Ampasambazimba (Lamberton, 1939); and a talus of *M. madagascariensis* was also recently recovered at Belo-sur-mer (Burney, personal communication). Among the new specimens from the Ankarana are two tali associated with the juvenile skeleton, two adult tali from individuals DPC 7821 and DPC 7950, each of which is associated with a calcaneus and numerous other pedal elements, and another isolated talus (DPC 10958). The new specimens from Ankilitelo include two tali from the associated juvenile hindlimbs (DPC 13733).

The *Megaladapis tali* (Fig. 6) are extremely variable in size but relatively consistent in overall morphology. The talar trochlea is deeply grooved (except in *M. edwardsi*) and asymmetrical, with the medial border extending further proximally than the lateral border. There is no posterior trochlear shelf as seen in extant prosimians, perhaps related to the large size of the flexor fibularis groove and the posterior extent of the trochlear articular surface (Decker and Szalay, 1974). The lateral border of the talar trochlea is flat and much shorter than the medial border. The facet for the lateral malleolus is flattened and triangular in shape. The flexor groove is extremely deep and strongly buttressed on either side. A prominent talar foramen is present and patent in most specimens. The proximal facet for the calcaneus is short, and it is rotated such that its long axis is directed more mediolaterally than proximodistally. The talar head is distinctively wide mediolaterally and dorsoplantary shallow. The neck is short in specimens of *M. edwardsi* and *M. grandidieri* but relatively longer in some specimens of *M. madagascariensis* (AM 45, AM 46).

M. edwardsi exhibits talar features distinct from the other species of *Megaladapis*. The talar trochlea and facets for the malleoli are especially flattened, leaving almost no demarcation of the trochlear borders. The sustentacular facets are also flattened and expanded. A similar flattening of the trochlear and sustentacular facets is seen in large-bodied African apes. The flexor groove is somewhat shallower, set more at an angle, and placed further laterally relative to the talar trochlea than in the smaller forms. Torsion of the talar head is also greatest in *M. edwardsi*. The two specimens of *M. madagascariensis* from Beavoha are the smallest tali, and the talar neck of these specimens is relatively long compared to the other *Megaladapis* specimens (including the new *M. madagascariensis* from Ankilitelo).

Talocrural joint function. The movements occurring at a typical talocrural joint are primarily plantarflexion and dorsiflexion. These movements, however, are defined as movements about a mediolateral axis; depending on the shape of the talocrural joint, movement at this joint also includes medial/

¹The Ampoza talus was initially misidentified as an element of *Palaeopropithecus* (Sera, 1935). Lamberton (1939) recognized its affinity with *Megaladapis*. He assigned it incorrectly to *M. grandidieri* but expressed doubts as to the species designation because of its provenience. Walker (1967) confirmed Lamberton's (1939) doubts and transferred it to *M. madagascariensis*.

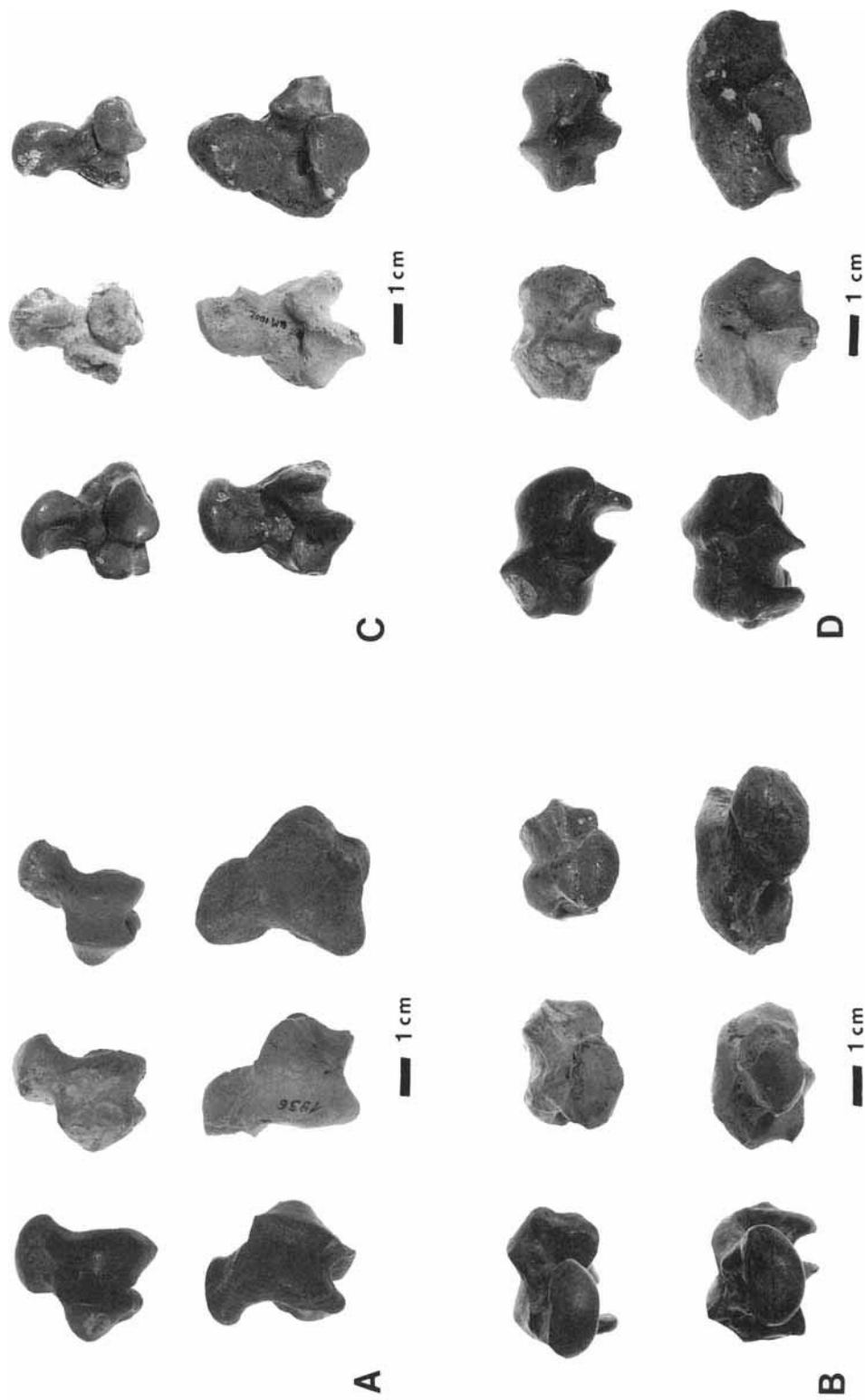


Fig. 6. *Megaladapis tali*, from left to right (top row) *M. edwardsi*, Manombo, Tulear; *M. edwardsi*, Beavohà; *M. grandidieri*, Ampasambazimba; (bottom row) *M. madagascariensis*, Beavohà; *M. sp.* (cf. *madagascariensis/grandidieri*), Ankarana; *M. madagascariensis*, Ampoza. A: Dorsal view. B: Plantar view. C: Distal view. D: Proximal view.

lateral rotation around a superoinferior axis (This movement is sometimes referred to as adduction/abduction. Strictly, however, the terms *adduction/abduction* refer to movement toward and away from the median sagittal plane or toward and away from the pedal or manual digital axes; use of the terms *adduction/abduction* is inappropriate with respect to the talocrural joint as they imply mediolateral sliding of the talus beneath the crus.), and supination/pronation around an anteroposterior (proximodistal) axis (Dagosto, 1985, 1986; Lewis, 1980a).

The talocrural joint of the small and intermediate-sized *Megaladapis* is a stable joint which undergoes medial and lateral rotation with dorsiflexion and plantarflexion. The longer medial than lateral trochlear ridge suggests that the tibia has a greater excursion medially than laterally. Due to the bony morphology of the talocrural joint, therefore, the tibia rotates medially (talus rotates laterally) during plantarflexion and laterally (talus medially) during dorsiflexion. The morphology of the triceps surae attachment also influences the rotational component of talocrural joint movement. When the triceps surae contract to plantarflex the foot, their medially placed insertion on the heel (see above description of the proximal calcaneus) simultaneously plantarflexes and inverts (laterally rotates and supinates) the hindfoot on the leg. The deep trochlear groove fixes and maintains the talocrural joint throughout this movement, and the higher lateral trochlear border provides stability at the talocrural joint in the inverted position by preventing lateral sliding or dislocation of the tibia on the talus.

The talocrural joint of *M. edwardsi* is similar in many aspects of morphology. The greatest difference from the smaller forms is the extreme flattening of the talar trochlear surface. Although it is unclear whether this flattening of the joint surface is indicative of a joint with a greater or lesser range of motion, it is clear that the movement at this joint was less fixed than it was in the smaller forms. Furthermore, this flattening of the joint surface was probably partly a function of body size in that a flatter joint provides a greater surface area upon which to distribute body weight; a similar degree of flat-

tening of the talocrural joint is seen in gorillas when they are compared to chimpanzees.

Subtalar joint function. Movement at a typical primate subtalar joint includes both rotation and translation of the calcaneus on the talus (if the foot is free) or of the talus on the calcaneus (if the foot is fixed). Rotational movement of the free foot, for example, is described as inversion and eversion, where inversion involves supination, medial rotation, and plantarflexion of the calcaneus on the talus and the opposite movements of the talus on the calcaneus. Due to the posterolateral and dorsomedial inclination of the axis of rotation of the subtalar joint, movement at the subtalar joint is a screw action in which the talus translates distally on the calcaneus during eversion and proximally on the calcaneus during inversion (Lewis, 1980b; Dagosto, 1986, 1988; Langdon, 1986).

Recall that in *Megaladapis* the sustentacular facets are proximodistally short and mediolaterally wide and that the proximal facet for the talus on the calcaneus is aligned at a strong angle to the long axis of the calcaneus. The proximal sustentacular facet on the talus is wide and concave mediolaterally and short and only slightly concave proximodistally, whereas the proximal facet for the calcaneus is convex mediolaterally and flat proximodistally. The shape of these facets suggests that relatively little proximodistal movement occurs with inversion and eversion at the subtalar joint but rather that the movements of inversion and eversion involve a great deal of supination/pronation and medial/lateral rotation at this joint. Such movements are similar only, among prosimians, to those seen in lorises which also have a joint offset from the long axis of the calcaneus (Dagosto, 1986); but even lorises do not appear to emphasize these movements to the extent seen in *Megaladapis*. Joints shaped for proximodistal movement, on the other hand, would be elongated proximodistally (Dagosto, 1986, 1988; Gebo and Dagosto, 1988), whereas the *Megaladapis* joints are short and wide.

Midtarsal region

The midfoot of *Megaladapis* is characteristically short relative to the large hindfoot

and forefoot regions. The distal tarsals are especially compressed proximodistally. Prior to the northern expeditions, these elements were unknown for *Megaladapis*. This region is now known from all elements in both the northern *M. sp.* (cf. *madagascariensis/grandidieri*) and *M. madagascariensis* from the southwest. The assemblage from the north includes three cuboids, four naviculars, three entocuneiforms, two mesocuneiforms, and three ectocuneiforms, all of which are associated with the other pedal elements. The remains from the southwest include three naviculars, three cuboids, entocuneiforms, and three ectocuneiforms.

Cuboid

There are six cuboids in the new collections, one from adult individual DPC 7950, two from the northern juvenile skeleton, one from the southern juvenile associated hindlimbs, and two more adult cuboids from the southwest belonging to a single individual (DPC 13663). The cuboid is relatively short proximodistally and wide proximally. In dorsal view, the medial side is considerably longer than the lateral side. The facet for the calcaneus is broad and dorsoplantarly shallow. It is convex medially and concave and narrower laterally. The peroneal groove is large but not as deep as that seen in most extant prosimians or most subfossil indroids. A strong plantar tubercle is present.

Among prosimians, only lorisines have a joint facet for the calcaneus on the cuboid shaped like that in *Megaladapis*, wide mediolaterally and short dorsoplantarly; however, lorisines differ considerably from *Megaladapis* in the morphology of the cuboid pivot. Lorisines have a long pivot which fits into a deep pit on the calcaneus (Dagosto, 1986; Gebo, 1986a), while *Megaladapis* has a relatively flat joint except for the small convexity medially and concavity laterally. Such a joint that is wide in one direction and narrow in the other and with little contour on each articular surface was probably not a very mobile joint in rotation, although some sliding was no doubt possible. The lorisine joint, although similar in outline, is highly mobile because of the almost ball-and-socket nature of the articulation between the cuboid pivot and the

calcaneal pit (Dagosto, 1986; Gebo, 1986a). The set of the calcaneocuboid joint in *Megaladapis* is extremely inverted (it should be noted that because of this set, use of conventional terms for mediolateral on the cuboid and the calcaneus make the mediolateral axes of these joints lie almost perpendicular to one another when the bones are articulated in the presumably habitually inverted position). The facet for the cuboid on the navicular is located plantarly on the lateral surface, and this position also contributes to the inverted position of the cuboid (see below and Fig. 7). Such a position is advantageous in grasping inasmuch as inversion of the cuboid brings the plantar surfaces of the fourth and fifth digits to face medially (i.e., toward the substrate).

Navicular

The navicular is extremely short and wide. The proximal articular surface is dorso-plantarly compressed and mediolaterally broad, corresponding to the shape of the talar head. In lorisines, such a joint shape is believed to be associated with a reduction in axial rotation (pronation/supination) at this joint. This reduction can take place because of the "preset" inverted position in these forms (Dagosto, 1986). The distal articular surface for the entocuneiform is large, flat, and oval in shape. The long axis of this facet runs parallel to the mediolateral axis of the navicular. In lorisines this same position is associated with a large angle of deviation between the first and second digits (Dagosto, 1986; Gebo, 1986a; Szalay and Dagosto, 1988). The facet for the entocuneiform encompasses more than half the area of the distal articular surface. The facet for the mesocuneiform is flat, rectangular, and makes no contact with the facet for the cuboid. The facet for the ectocuneiform is semicircular in shape and separated from that of the mesocuneiform by a ridge. The facet for the ectocuneiform is positioned laterally and is separated by a ridge from the facet for the cuboid. The *Megaladapis* navicular is distinct from all other prosimians in its proximodistal reduction in length and in the relative breadth of the proximal facet.

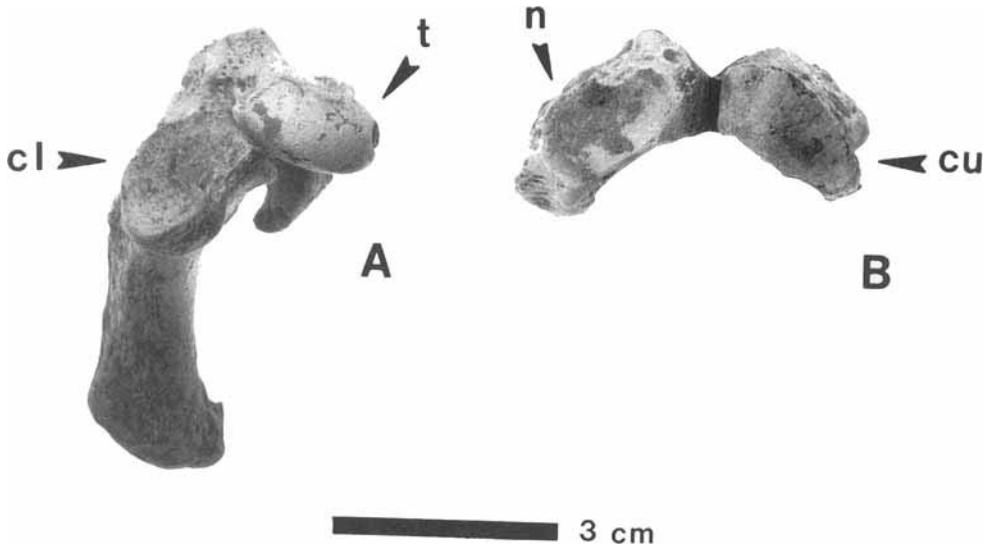


Fig. 7. Open view of the transverse tarsal joint of *Megaladapis* cl, distal calcaneus, facet for cuboid; cu, proximal cuboid; n, proximal navicular; t, talar head. **A:** Distal view of calcaneus and talus in an inverted position. Note the dorsoplantarly shallow and mediolaterally broad talar head, the high and narrow cuboid facet on the calcaneus, and the position in which the distal calcaneus is placed such that the dorsal cuboid will face laterally and the fourth and fifth metatarsals will be positioned with their plantar surfaces facing medially. The distal surfaces of the talus and calcaneus form half of a

serial joint in that they extend distally to the same level, forming essentially one joint surface. **B:** Proximal view of the navicular and cuboid. The navicular and cuboid are dorsoplantarly shallow and mediolaterally wide, matching the shapes of the talar head and distal calcaneus, and thereby probably allowing little rotation and mostly translation at the joint. The proximal cuboid is fairly flat and articulates plantarly on the navicular, forming with the lateral cuneiforms a high transverse tarsal arch.

Transverse tarsal joint function. The narrow articulation between the talus and the navicular is indicative of a joint undergoing little to no axial rotation but mostly mediolateral translation. Such mediolateral translation of the talar head on the navicular presumably occurs during extensive inversion/eversion movements that are occurring at both the transverse tarsal and the subtalar joints. During inversion, the talar head moves laterally and dorsally on the navicular. The transverse tarsal joint is relatively uninhibited in its mediolateral movement because of its serial construction. During inversion the navicular-cuboid complex supinates, leaving the lateral talar head in contact with the lateral portion of the proximal navicular facet and the calcaneocuboid joint positioned beneath the navicular. In this position the distal cuboid facets are oriented in such a way as to leave the plantar surfaces of the fourth and fifth metatarsals facing

inward toward the substrate. Such a position is ideal for grasping vertical supports or for underbranch (antipronograde) positional behaviors.

Cuneiforms

The cuneiforms are short and blocky. The first cuneiform is mediolaterally narrow and positioned such that the long axis of the first metatarsal joint runs proximodistally and the joint itself faces medially. The *Megaladapis* entocuneiform resembles the lorisine condition in some respects such as orientation and the relative position of the first metatarsal and navicular joint surfaces. Lorisines are the only extant prosimian taxa to exhibit a facet for the navicular that is not more or less parallel to that for the first metatarsal but rather is set at an angle to increase abduction of the first metatarsal (Grand, 1967; Dagosto, 1986; Gebo 1986a, 1989b). Gebo (1989b, p. 355) attributes this

feature to "an adaptation for grasping larger diameter supports relative to foot size." The differences between the lorisine entocuneiform and that of *Megaladapis* are primarily in the excessive proximodistal compression of the *Megaladapis* entocuneiform so as to bring the proximal ends of the first metatarsal joint and the distal end of the navicular joint into close proximity (see Fig. 2).

The mesocuneiform is short such that a notch is created for the second metatarsal base, with the entocuneiform and ectocuneiform forming the sides of the notch. The ectocuneiform is wedge-shaped, being longer laterally than medially and, therefore, extending further proximally laterally. It articulates far laterally on the navicular, dorsal to the cubonavicular articulation. Such a lateral articulation and wedge shape allow for a steep transverse tarsal arch across the cuneiforms. The ectocuneiform has a large dorsal and a small plantar articulation with the cuboid.

Metatarsals and phalanges

Metatarsals and phalanges of *Megaladapis* are fairly well known in the literature and have formed the basis for many former discussions of the positional repertoire of *Megaladapis*. Because the lateral metatarsals and phalanges have already been extensively described, we will not discuss them in detail here, but rather we refer the reader to descriptions in Lorenz von Liburnau (1905), Lamberton (1939), Ekblom (1951), Walker (1967, 1974), Jungers (1976) and Preuschoft (1971). Metatarsals II–V are robust but long relative to most tarsal elements. The proximal phalanges are long and moderately curved (Jungers et al., 1994). Total digit lengths are long relative to tarsals and the entire hindlimb. They serve to reinforce the overall impression of a powerful grasping organ (Walker, 1967; Jungers, 1976).

Although the first metatarsal has also been used in earlier interpretations of the locomotor repertoire of *Megaladapis* (e.g., Lorenz von Liburnau, 1905; Lamberton, 1946; Ekblom, 1951; Walker, 1967, 1974; Jungers, 1976), very few specimens of the first metatarsal of *Megaladapis* have been described, and most of those that have been discussed are not even first metatarsals. Lo-



Fig. 8. Adapted from Lorenz von Liburnau's (1905) illustrations of the first metatarsal of *Megaladapis edwardsi*. These are the only specimens presently attributed to this taxon and are somewhat enigmatic. The morphology of the distal articular surface of the first metatarsal is unlike the specimens of *M. sp.* (cf. *madagascariensis/grandidieri*) or *M. madagascariensis*.

renz von Liburnau (1905) described and figured a damaged specimen that he called the first metatarsal of *Megaladapis edwardsi*; it measured over 80 mm in length (Fig. 8). Lamberton's (1946) specimens are approximately 47 mm in length and were nevertheless also attributed to *Megaladapis edwardsi*. The specimen described as *Megaladapis edwardsi* by Ekblom is 52.4 mm in length. Based on the relative proportions of the metatarsals and the morphology of the proximal end, Jungers (1976) suggested that the specimens at the Académie Malgache (Lamberton, 1946) and at Uppsala (Ekblom, 1951) were first metacarpals of *M. edwardsi*. A new first metacarpal from the southwest that is almost identical in size and morphology (Table 2) to the Académie Malgache and Uppsala specimens indicates that all previously putative first metatarsals (except that in Lorenz von Liburnau, 1905) are, in fact, metacarpals of *M. madagascariensis*.

TABLE 2. First metacarpal and metatarsal dimensions of *Megaladapis*¹

Specimen/source	Maximum length (mm)	Breadth—proximal (mm)	Breadth—distal (mm)	Attribution
Uncataloged—SP, (Beavoha 1936)/Lamberton, 1946	47.0	20.0	16.0	<i>M. madagascariensis</i> R. metacarpal
Uncataloged—SP, (Beavoha 1936)/Lamberton, 1946	46.8	20.0	16.0	<i>M. madagascariensis</i> L. metacarpal
PIUP 19/Ekblom, 1951	52.4	26.0	22.9	<i>M. madagascariensis</i> R. metacarpal
VMNH/Lorenz von Libumau, 1905	>80	—	26	<i>M. edwardsi</i> L. metatarsal
DPC 7950	57.7	25.5	21.5	<i>M. madagascariensis</i> / <i>grandidieri</i> R. metatarsal
DPC 7821	57.8	25.5	22.1	<i>M. madagascariensis</i> / <i>grandidieri</i> L. metatarsal
DPC 7863	>56.4	25.9	21.0	<i>M. madagascariensis</i> / <i>grandidieri</i> L. metatarsal
DPC 13744	>56.6	28.7	19.3	<i>M. madagascariensis</i> R. metatarsal

¹DPC, Duke University Primate Center (Durham, NC); PIUP, Paläontologischen Institut der Universität (Uppsala, Sweden); SP, Service de Paléontologie, Université d'Antananarivo (Madagascar); VMNH, Naturhistorisches Museum, Paläontologische Abteilung (Vienna, Austria).

This view is confirmed by the morphologically similar first metacarpals from the north belonging to *M. sp.* (cf. *madagascariensis/grandidieri*).

Three adult and two juvenile first metatarsals are present in the new collections from northern Madagascar. One specimen (DPC 7950) is associated with proximal and distal phalanges as well. The southwestern specimens include one isolated first metatarsal (DPC 13744) which is very similar in size and morphology to the first metatarsals from the north. Measurements of these specimens in comparison to the specimens formerly attributed to *M. edwardsi* are presented in Table 2.

The first metatarsal is a robust bone. The proximal articular surface is broad mediolaterally and narrow dorsoplantarly. The peroneal tubercle is small relative to those seen in most extant prosimians. The distal articular surface is broad and expanded laterally to a tubercle for the attachment of the adductor musculature. The proximal phalanx is also robust and dorsoplantarly flattened. The proximal end exhibits a tubercle for the adductor corresponding to that on the distal metatarsal. The distal phalanx is very large, with an expanded base and rugose apical region.

Although the peroneal tubercle on the base of the first digit metatarsal is relatively

small, that on the base of the fifth metatarsal is large in all dimensions and is rounded. It should be noted that this tubercle serves not only as the insertion site for the peroneus brevis muscle but also as the insertion site for the abductor os metatarsi muscle. This muscle originates on the lateral side of the proximal calcaneus and inserts onto the base of the fifth metatarsal tubercle laterally. Its function is presumably to abduct (laterally deviate) the lateral border of the foot (Gebo, 1986b). Such an action (along with the same action being performed further distally by the fifth digital abductor) is advantageous when climbing up and clinging to vertical supports in that it acts to resist gravitational forces tending to adduct the abducted first and lateral digits (Cartmill, 1974). The abductor os metatarsi muscle also probably acts with the fifth digital abductor to place the forefoot in a laterally deviated position, whereby the fifth digit abductor can help to flex the fifth digit and thereby enhance grasping effectiveness (Gebo, 1985, 1986b). Based on the small size of the hallucial peroneal tubercle, the modest development of the peroneus longus groove on the cuboid, and the proximodistally restricted peroneal tubercle on the fifth metatarsal of the small and intermediate sized forms, we suspect that peroneal development in *Megaladapis* was deemphasized in favor of the intrinsic



Fig. 9. Fifth metatarsals of *M. madagascariensis* (left two), *M. sp.* (cf. *madagascariensis/grandidieri*) (middle), and *M. edwardsi* (right 2). In *M. madagascariensis* and *M. sp.* (cf. *madagascariensis/grandidieri*), the tubercle at the base of the fifth metatarsis is bulbous and positioned lateral to the proximal articular surface, separated from the articular surface by a groove. In *M. edwardsi* the tubercle is a ridge positioned further distally.

abductors (except, perhaps, in *M. edwardsi* [see below]). The intrinsic abductors might be preferred over the peroneals in supplementing the flexors of the first and fifth digits and in abducting the lateral border of the foot because they are not affected by the position of the leg, and they do not produce simultaneous eversion. The fifth metatarsal tubercle exhibits a remarkable difference in morphology between the larger *M. edwardsi* and the smaller forms. In *M. madagascariensis*, *M. grandidieri*, and *M. sp.* (cf. *madagascariensis/grandidieri*) the tubercle is bulbous in shape, is positioned lateral to the proximal articular surface, and is separated from the articular surface by a groove. In *M. edwardsi*, on the other hand, the tubercle is positioned distally on the shaft relative to the articular surface, and it takes the form of a ridge rather than a bulbous projection (Fig. 9). The differences in tuberosity position and shape may be functionally related to the relative size of the muscles attaching to this tubercle. The peroneus brevis muscle inserts laterally on the peroneal tubercle. The abductor os metatarsi muscle attaches proximally to the tubercle and seems to have

had more influence on the development of this tubercle in the small and intermediate-sized forms.

First metatarsal-entocuneiform joint function. The morphology of the first metatarsal-entocuneiform joint of primates is quite variable and has been described extensively by Szalay and Dagosto (1988). These authors realized the need for material from the giant subfossil primates: "The potentially most interesting taxa, such as *Megaladapis* and the palaeopropithecines . . . are unknown in this regard" (p. 16). The *Megaladapis* joint is shallow, mediolaterally broad and dorsoplantarly narrow and faces medially. The shape of the joint restricts movement to a stereotypical direction. Although flexion/extension is accompanied by some medial and lateral rotation, there is virtually no pure abduction/adduction component to movement at this joint. Structural abduction of the hallux is a function of the relationship among the facets (first metatarsal, second metatarsal, and navicular) on the entocuneiform. In the new *Megaladapis* specimens, the relative positions of the facets for the

navicular and first metatarsal on the entocuneiform resemble the arrangement seen in lorises, resulting in a widely abducted hallux position (Gebo, 1986a, 1989, 1993; Szalay and Dagosto, 1988). Because of the widely abducted set to this joint, flexion/extension occurs in pincer-like opposition to the lateral digits and allows a wide-spanning grasp that can subtend large central angles (and thereby increase friction) on any arboreal support (Cartmill, 1974).

Hindlimb and pedal proportions

The abundance of associated remains among the new material allows closer examination of proportional relationships within the hindlimb and within the foot itself. The following discussion of proportions is based on material from the subadult skeleton from the Ankarana (DPC 9089) because of its completeness and association. Based on direct comparisons between homologous elements in the subadult skeleton and those in a partial adult specimen (DPC 7950), the immature nature of this specimen appears to have little impact on aspects of relative size and shape. For example, the ratio of first metatarsal length to tibia length is 0.35 in both, and the ratio of calcaneus plus cuboid length to tibia length is 0.51 and 0.49 in the subadult and adult, respectively.

The foot of *Megaladapis* is exceptionally large, measuring roughly 45% the length of the hindlimb. This relative length is longer than for any living primate (Fig. 10), approximated most closely by the orangutan at 38%. This ratio is affected greatly, however, by the relative shortness of the hindlimb in *Megaladapis* (Jungers, 1977, 1978). The hallux itself measures over 80% the length of the tibia in the only adult specimen in which all these elements are in association (Fig. 11). The foot is clearly an essential element of the hindlimb mechanism for support and propulsion; interpretation of the mechanism of grasping and propulsion warrants the examination of intrinsic proportions of the foot.

Although superficial inspection suggests that the calcaneus is fairly large, the tarsus of *Megaladapis* makes up only 29–30% of the foot length. This value is similar to that seen in indrids, *Daubentonia*, and lorises and is smaller than that of lemurids, gala-

gines, and most anthropoids. Long tarsals are seen in small-bodied prosimian leapers such as *Galago* and *Tarsius* who elongate the distal portion of the calcaneus. *Gorilla* and *Homo* also elongate the tarsus but do so proximally, perhaps in association with the plantigrade position of the foot (Jouffroy and Lessertisseur, 1979). Among New and Old World monkeys, calcaneal elongation is associated with quadrupedalism, presumably to increase the length of the hindlimb load arm (Rose, 1986). The relative shortness of the *Megaladapis* tarsus is due in part to the short distal tarsal region and in part to the long metatarsal and phalangeal region. Relative digit length (metatarsal 4 + digit 4 as a percentage of foot length) is high relative to most extant prosimians and anthropoids, again resembling indrids, lorises, and *Daubentonia*. The relatively short tarsus of *Megaladapis* is suggestive of a foot used less as a lever and more as a grasping organ; the relatively large proximal calcaneus (see below), the long and robust hallux, and long, curved proximal phalanges support this assessment.

The relative proportions of the regions of the calcaneus have frequently been used in interpretations of pedal morphology (Walker, 1970; Gebo, 1986a; Rose, 1986; Gebo and Simons, 1987; Gebo and Dagosto, 1988; Strasser, 1988). Among prosimians, galagos and tarsiers exhibit exceptionally long distal calcanei associated with their tarsal-dominated leaping habits, while lorises and indrids have relatively short distal calcanei (Gebo, 1986a; Gebo and Simons, 1987). Anthropoids tend to have distal calcanei at least as short as these latter taxa. Among anthropoids, hominoids (especially great apes) tend to have relatively shorter distal calcanei, while, in general, New and Old World monkeys have longer distal calcanei (Rose, 1986; Gebo and Simons, 1987). Prosimian taxa with short distal calcanei tend to elongate the middle calcaneus rather than the proximal calcaneus (Gebo, 1986a,b; Gebo and Simons, 1987). *Megaladapis* has an extremely short distal calcaneus (distal length = 36% total length), below all living prosimians in this proportion. The middle calcaneus, however, is also short (middle length = 27% total length), but the prox-

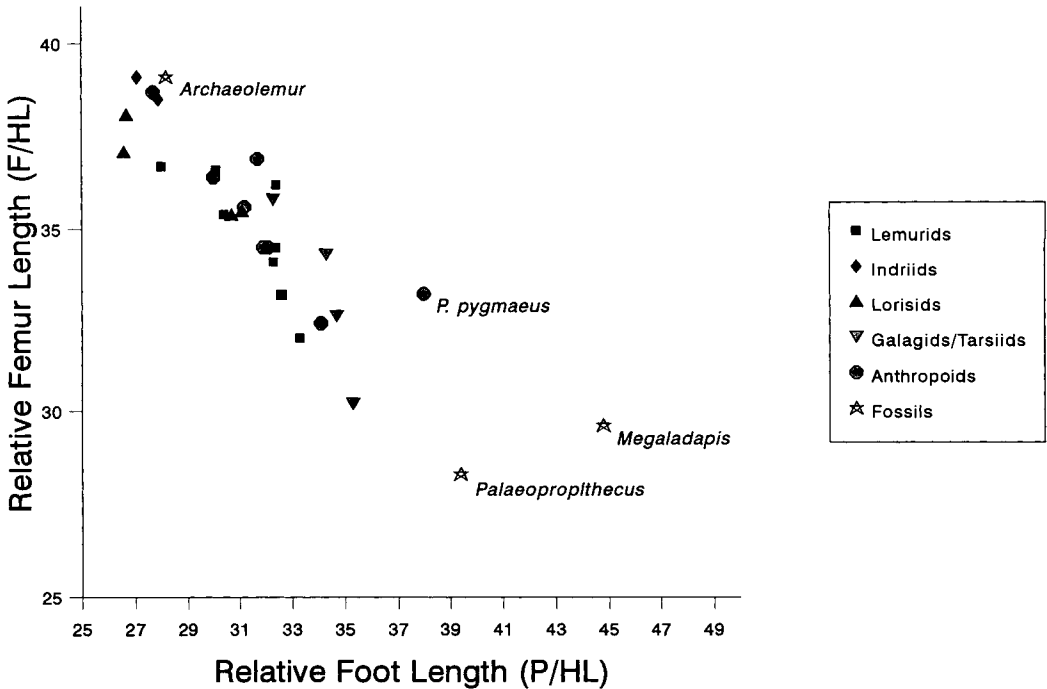


Fig. 10. Hindlimb proportions distinguish *Megaladapis* as having a very long foot relative to total hindlimb length. The closest living primate in relative foot length is the orangutan. Hindlimb length is taken as the sum of the lengths of the femur, tibia, and foot. Foot length is the maximum length, which is taken as the sum of

the lengths of calcaneus, cuboid, and metatarsal and phalanges of the longest digit (usually fourth in prosimians and third in anthropoids). (Extant data from Jouffroy and Lessertisseur, 1978, 1979; also see Lessertisseur and Jouffroy, 1973, and Schultz, 1963).

imal calcaneus is very long (proximal length = 37% total length). In relative proximal calcaneal length, *Megaladapis* exceeds all living prosimians (Fig. 12). Living primates resembling *Megaladapis* in the relative proportions of the calcaneus include *Gorilla*, *Pongo*, *Pan*, and *Alouatta* (Gebo and Simons, 1987). As discussed above, calcaneal elongation is associated with lengthening the hindlimb load arm in quadrupedalism (Rose, 1986). Elongation of this sort occurs in the distal calcaneus, anterior to the fulcrum (the talocrural joint). Distal calcaneal elongation is expected and seen, therefore, in animals using a great deal of arboreal or terrestrial quadrupedalism or tarsi-fulcrimated leaping. Vertical climbing and suspension benefit less from such distal elongation, and therefore lorises, large hominoids, and *Megaladapis* exhibit shortened distal calcanei. Proximal calcaneal elongation in *Megaladapis* may have been

due in part to the great development of the musculature originating on the proximal calcaneus and the underlying plantar fascia. Also, proximal calcaneal elongation was probably associated with the powerful "lever action" of the triceps surae which tended to invert and plantarflex the foot and maintain such a position during grasping. As discussed above, the morphology of the heel process in *Megaladapis* suggests great development of the abductor musculature, especially that to the fifth digit.

Summary of features and assessment of function in the *Megaladapis* foot

The importance of cheiridial functional morphology to the interpretation of positional behavior and substrate use in extinct primates is well recognized. The cheiridia are valuable indicators of positional adaptation in that they directly contact the diverse structural environment in which primates



Fig. 11. Associated tibia and hallux of *Megaladapis* sp. (cf. *madagascariensis/grandidieri*) (DPC 7950). The hallux of *Megaladapis* is over 80% the length of the tibia.

characteristically move, and they form the link through which forces are transferred between the animal and the physical or mechanical environment. Jouffroy and Lestertisseur (1979) summarized the importance of the analysis of cheiridia to evolutionary studies:

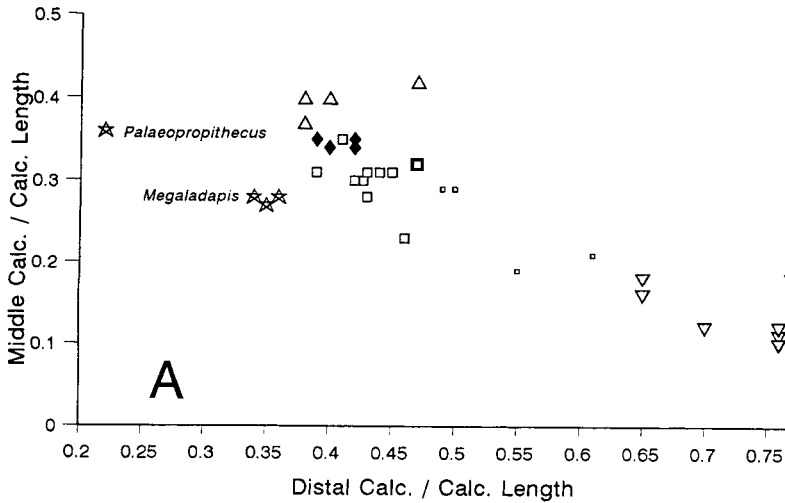
Because they are the organs of support and of contact between the animal and its environment during both locomotion and prehension, they express, more than

any other element of the locomotor apparatus, the adaptations that have incontestable evolutionary and taxonomic significance.

The *Megaladapis* foot is unique among primates in its large size and powerful grasping mechanism. New pedal remains provide insight into the mechanism of grasping and of weight transfer through the foot. Below, we summarize the prominent features of each region of the foot and then present inferences as to how the regions of the foot function together during posture and locomotion.

The *Megaladapis* foot is notable, first, in its extremely large size relative to the hindlimb. The hindfoot is large, especially in its proximal-most portion. Prominent muscle attachments suggest that this region functioned at least partially to power inversion and an abduction/flexion-type grasp. Such modifications appear to be one way for prosimians to deal with large body size in an arboreal environment and are very different from the anatomical solution to arboreality used by the contemporaneous sloth lemurs (Wunderlich et al., 1993, 1994). The *Megaladapis* foot also exhibits a great deal of medial and lateral rotation and supination/pronation movements relative to translational movements at the talocrural, subtalar, and transverse tarsal joints. Morphological features indicative of the high capacity for inversion and eversion include the serial tarsus, the short, wide, and obliquely set (proximal) sustentacular facets, the medially expanded heel process which aligns the triceps surae medially, the twisted, asymmetrical talar trochlear surface, and the plantarly directed facet for the cuboid on the navicular. Most remarkable, however, is not the mobility of the joints in inversion and eversion or the powerful abductor musculature but rather the way in which *Megaladapis* has emphasized these movements to the extent of designing the joints to virtually fix movements along certain pathways. The deep trochlear groove, along with asymmetrical margins, in *M. madagascariensis*, *M. grandidieri*, and *M. sp.* (cf. *madagascariensis/grandidieri*), for example, fixes movement at the talocrural joint in a path of tibial plantarflexion/medial rotation or dorsiflexion/lateral rotation. The short, nar-

Calcaneal Proportions Distal vs. Middle



Calcaneal Proportions Distal vs. Proximal

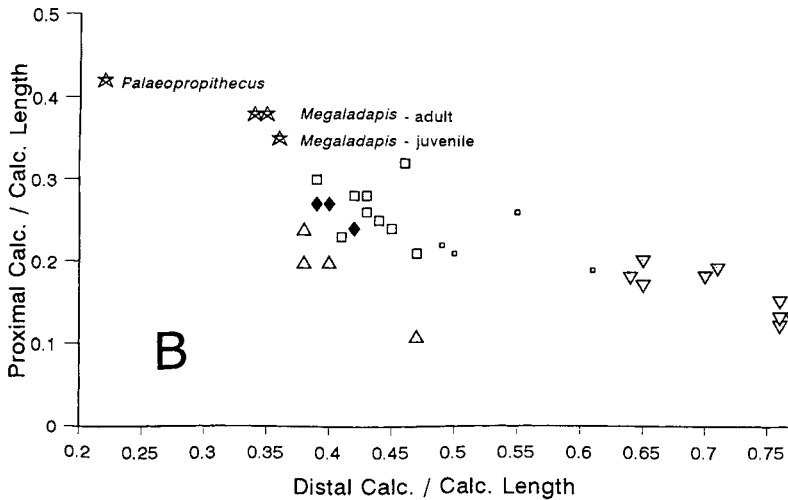


Fig. 12. Relative calcaneal proportions distinguish *Megaladapis* among prosimian primates. **A**, distal vs. middle proportions; **B**, distal vs. proximal proportions. The relative length of the anterior calcaneus (distance from the distal end of the proximal sustentacular facet to the distal calcaneus) is extremely short, while that of the posterior calcaneus (distance from the proximal end of the proximal facet to the proximal calcaneus) is

quite long, exceeding all living primates in both relative lengths. The adult specimens from the north and the southwest are very similar in relative calcaneal proportions. Lorisids share with *Megaladapis* a short anterior calcaneus but tend to lengthen the middle calcaneus over the posterior. (Extant data partially from Gebo, 1986a; Gebo and Simons, 1987.)

row proximal navicular facet has been reduced to accommodate almost exclusive lateral and medial translation of the talar head on the navicular with little axial rotation at this joint. Finally, the first metatarsal-entocuneiform joint is expanded in one direction and restricted in the others such that hallucal movement is essentially fixed in a path of almost pure flexion/extension with some axial rotation but little abduction or adduction.

The function of the *Megaladapis* foot as a whole must be considered in terms of grasping as well as in terms of weight transfer through the foot during locomotion. The *Megaladapis* foot seems extremely well designed for grasping vertical supports of any size, but a variety of arboreal postures, including quadrupedal hanging and pedal suspension, were likely feasible because of its powerful grasping mechanism. The large, widely abducted hallux will allow the foot to subtend large angles on all supports. The inverted set of the transverse tarsal joint positions the midfoot and forefoot in a position optimal for grasping in which the plantar surfaces of the lateral digits are rotated to face into the substrate. Finally, the powerful abductors of the fifth and probably first digits allow *Megaladapis* to take advantage of a uniquely prosimian arrangement of muscle attachments that is especially well suited to climbing upon and clinging to vertical supports. The fifth digit abductor as well as the abductor os metatarsi muscle abduct the lateral border of the foot, and the abductor of the fifth digit also acts as a flexor. In this way, the first and fifth digits are simultaneously abducted and flexed, thereby generating adequate friction while resisting the tendency of gravity to adduct the digits.

Although the *Megaladapis* foot is well adapted to climbing large vertical supports (Walker, 1974; Jungers, 1977, 1978), it was clearly not restricted in any way from use on supports of different size and orientation. During the support phase of vertical climbing the tibia is rotated over the talar trochlea from a position near neutral to full dorsiflexion. The push-off phase follows and involves rotation from dorsiflexion into full plantarflexion, at which point swing phase begins. During this weight transfer over the

stationary foot, the foot must maintain its grasp on the support. The *Megaladapis* foot is constructed to maintain this grasp during the stance phase. The medial attachment of the triceps surae on the large, medially directed heel process produces a large inversion component to plantarflexion, maintaining the grasping position of the foot during translation of the leg over the foot. Meanwhile, the powerful abduction flexion grasp which utilizes the intrinsic abductor musculature maintains a powerful grasp regardless of the position of the leg. Finally, because the foot remains in this abducted, inverted grasping position during plantarflexion, the tibia must medially rotate during plantarflexion in order to transfer weight over the foot in the direction of travel. The talocrural joint is designed for this medial rotation of the tibia on the talus during plantarflexion.

Other regions of the anatomy of *Megaladapis* are also indicative of a positional repertoire emphasizing slow climbing. Analyses of the hindlimb and pelvic anatomy as well as of the limb proportions of *Megaladapis* (Jungers, 1977, 1978) have demonstrated that *Megaladapis* conforms well to the vertical support model for clawless mammals (Cartmill, 1974). In the present study we have attempted not only to categorize the positional behavior and substrate preferences of this large subfossil lemur but also to hypothesize about the mechanism by which it grasped and moved within this environment. These hypotheses have been made through theoretical associations based on comparative morphology and speculation about joint and muscle function; experimental analyses of these mechanisms in living primates will be necessary to test and refine these hypotheses.

Finally, the interpretations of function presented here have been based primarily on evidence from *Megaladapis* sp. (cf. *madagascariensis/grandidieri*) from the north and the newest remains of *M. madagascariensis* from the southwest. Although these specimens closely resemble one another and *M. grandidieri* from central Madagascar in morphology and probably function, the large *M. edwardsi* clearly exhibits features of the talus that are quite different

from the other forms and which could be suggestive of a greater degree of terrestriality if gorilla-chimpanzee analogies are appropriate. Furthermore, the difference in size and shape of the tuberosity of the fifth metatarsal suggests differential development of the intrinsic abductor mechanism (with the smaller forms being more highly developed in this regard). The long, moderately curved phalanges of *M. edwardsi*, high intermembral index, and other anatomical details of the appendicular and axial skeleton, however, are still indicative of capable and frequent arboreality in this large folivore. Additional pedal remains from *M. edwardsi* will no doubt shed new light on the total range of positional behaviors used by this extinct genus.

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